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SHORT COMMUNICATION

Variation in web-building spider communities among three tropical tree species in a young experimental plantation

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Abstract. We documented the presence and abundance of spider species (Arachnida: Araneae) on young trees of *Swietenia macrophylla*, *Ceiba pentandra* and *Cordia dodecandra* found in an experimental plantation. Surveys of spider abundance and species identity conducted twice during the growing season indicated marked differences in web-building spider assemblages associated with each tree species. *Swietenia* exhibited the lowest spider abundance, whereas *Cordia* and *Ceiba* had similarly higher abundances. *Leucauge venusta* (Walckenaer, 1841) was the dominant spider on all tree species, but different spider species were co-dominant on *Cordia* and *Ceiba* (*Araneus pegnia* (Walckenaer, 1841) and *Argiope argentata* (Fabricius, 1775) respectively), and several spider species were exclusive to each tree species. These results highlight the influence of tree species identity on community structure at higher trophic levels, particularly in the case of web-building spiders inhabiting tropical tree communities.

Keywords: Abundance, Araneae, plant traits, predator, species composition

The effects of plant phenotypic variation on consumer communities have been extensively documented (Mooney & Singer 2012). Such effects are generally attributed to plant genotypes or species varying in associated key traits, for example, chemical defenses and nutritional quality for herbivores or refuge availability for mutualists (Karban 1992; Mooney & Singer 2012). Within this context, research on the consequences of plant species variation on herbivores has historically received much attention particularly for herbaceous plants (Hunter et al. 2000). In contrast, fewer studies have rigorously evaluated tree species variation in associated consumer communities despite the fact that arboreal plants dominate many types of terrestrial ecosystems, and few of these studies have looked at effects on predators and parasitoids (for exceptions see: Lill et al. 2002; Vehviläinen et al. 2008; Singer et al. 2014).

Spiders (Araneae) are one of the most diverse and abundant invertebrate predators in terrestrial ecosystems (Platnick 2015). Within this order web-building spiders, which represent ca. 30% of all spider species, are ubiquitous predators in terrestrial food webs (Pp. 25–38, 68–74 & 235–243 in Ubick et al. 2005). Plant species variation in web-building spider communities is strongly and directly mediated by plant physical traits such as leaf position, thickness, or branch/leaf architecture which determine site-choosing preferences for web-building (Langelloto & Deno 2004; Jiménez-Valverde & Lobo 2007), as well as by the availability of refuges from other predators (Gunnarsson 1990; De la Cruz et al. 2009). However, the effects of arboreal species identity on spiders have been poorly studied despite the fact that long-lived tree species vary substantially in many of the aforementioned traits and presumably provide ample opportunity for bottom-up effects on predator abundance and diversity.

We report on the results of a study conducted in a four-year-old experimental tree planation in Yucatán, México. We used a subset of plots for this experiment, containing big-leaf mahogany (*Swietenia macrophylla* King), *Ceiba pentandra* (L.) Gaertn, and *Cordia dodecandra* A. DC., and evaluated whether there were differences in the web-building spider assemblages recruiting to these tree species. We expected that differences among tree species in physical traits (e.g., architecture, size, leaf arrangement) would lead to variation in spider abundance and species composition.

The plantation was established in December 2011 at a site in Yucatán, México (20°24′44″N, 89°45′13″W), and included six tree species: *Swietenia macrophylla* King (Meliaceae), *Tabebuia rosea* (Bertol.) DC. (Bignonaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A. DC. (Boraginaceae). Seeds were collected from adult trees located in southern Quintana Roo (México), and seeds from a single parental tree represented a maternal source. For details see: Abdala-Roberts et al. (2015).

The plantation consisted of 74 plots, 21×21 m each, with a planting density of 64 plants per plot and 3-m spacing among trees, for a total of 4780 trees. Plots were classified as species monocultures or polycultures, the latter composed of random mixtures of four out of the six species (Abdala-Roberts et al. 2015). We selected three out of the six tree species for this study, namely: *S. macrophylla* (hereafter *Swietenia*), *Cordia dodencandra* (hereafter *Cordia*), and *Ceiba pentandra* (hereafter *Ceiba*), as these species exhibit marked differences in chemical traits (e.g., phenolics) (Moreira et al. 2014; Abdala-Roberts et al. 2015; S. Rosado-Sánchez, unpublished) which might influence herbivore recruitment, as well as in physical traits (e.g., branching pattern and canopy cover) which may influence web-building spiders (Table S1, online at http://dx.doi.org/10.1636/JoA-S-16-016.s1). For this study, we used seven polyculture plots within which these species were present, in addition to a fourth species (*T. rosea*, *P. piscipula*, or *E. cyclocarpum*) which was not sampled and varied in identity across plots (see Table S2, online at http://dx.doi.org/10.1636/JoA-S-16-016.s1). The selected plots were the only polycultures where the three focal species co-occurred.

We conducted two surveys of web-building spiders, one in May 2013 and another in September 2013. During each survey, we sampled the same plots but inspected a different set of trees within each plot because collection of spider specimens during the first survey could influence spider abundance or species composition during the second survey. For each plot, we randomly sampled a total of 20 trees across both surveys (10 trees per plot, per survey) (see Table S2). At the time of sampling, trees were two (*Cordia*) to four (*Ceiba*, *Swietenia*) m tall. To reduce edge effects on spider recruitment, we avoided plants located on the outer rows of each plot. Across plots and surveys, a total of 140 plants were sampled: 42 for *Swietenia*, 52 for *Ceiba*, and 46 for *Cordia*.

Surveys were conducted in the morning (700 to 1300 hrs) by "looking down", in which the plant is inspected from ground level up to a height of 0.5 m, and then "looking up" by continuing the search up to two m of height (Coddington et al. 1991). This resulted in a thorough sampling of the main stem and the lower- to mid-portion of the canopy of all the trees. The examination of each plant lasted six minutes and we recorded all web-building spiders regardless of web structure. Specimens were preserved in 70% ethanol and transported to the laboratory for species identification using specialized literature (e.g., Levi 1955, 1978, 1991; Ubick et al. 2005). Scientific names were updated using the World Spider Catalog (Platnick 2015). Unidentified individuals were classified as morphospecies.

To test for differences among tree species in spider community composition, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2001) in the VEGAN package of R ver. 3.0.2 (R Core Team, 2013) with 1000 random permutations using a dissimilarity distance matrix with spider species abundances based on the Jaccard index (Chao et al. 2006). We previously ran this analysis restricting the permutations to each plot ("strata" option) to account for spatial structure (i.e., autocorrelation) and results remained unchanged; therefore, we report results for the unrestricted analysis.

We tested for tree species differences in spider abundance with a generalized linear mixed model using a Poisson distribution and log link in PROC GLIMMIX, SAS version 9.2 (SAS Institute 2009, Cary NC). We used data at the plant level and included tree species (fixed effect), survey (random), plot (random), and maternal source (random, nested within plot) as independent variables. This analysis was repeated excluding the most abundant spider (*Leucuage venusta* (Walckenaer, 1841)) to determine whether tree species differences were driven by this spider. We compared differences between tree species means using Bonferroni-adjusted least-square means.

A total of 426 spider specimens were collected across all tree species, representing four families, 24 genera, and 28 species (Table 1). The family Araneidae had the highest species richness with 14 species, followed by Theridiidae with 12 species. The families Uloboridae and Tetragnathidae were each represented by only one species. The most common species were *Leucauge venusta* with 231 individuals (54.2% of the sample) and *Araneus pegnia* (Walckenaer, 1841) with 54 individuals (12.6%).

Results from the PERMANOVA indicated a significant effect of tree species on spider species composition ($F_{2,91} = 3.29$, $P < 0.001$). With the exception of *L. venusta*, which was consistently the most common species on all tree species, we found that the composition and relative abundance of the following most abundant spider species varied among tree species. For *Swietenia*, the second most abundant species was *Eriophora ravilla* (C. L. Koch, 1844) representing 9% of the specimens sampled on this tree species, whereas for *Ceiba* the second most abundant species was *Argiope argentanta* (Fabricius, 1775) (11%) and for *Cordia* it was *Araneus pegnia* (23%). A follow-up (2 by 2) contingency table indicated a significant association of *Arg. argentata* and *Aran. pegnia* abundance with *Cordia* and *Ceiba*, respectively ($\chi^2 = 37.71$, df = 1, $P < 0.0001$). We found a similar number of rare species (i.e., represented by one individual for each tree species) on all tree species (eight for *Swietenia* and seven each for *Ceiba* and *Cordia*), but many of these were exclusive to each tree species (see Table 1).

For spider abundance, *Cordia* accounted for 42% ($n = 182$) of all specimens recorded, followed by *Ceiba* with 33% ($n = 142$) and *Swietenia* with 25% ($n = 102$) (Table 1). The generalized linear mixed model indicated a significant effect of tree species on the abundance of web-building spiders per plant ($F_{2,14} = 11.55$, $P = 0.001$). There was also a significant effect of tree species on spider abundance after excluding *L. venusta* ($F_{2,14} = 5.93$, $P = 0.013$), suggesting that tree species differences were not predominantly driven by this dominant spider species. Comparison of least-square means (model including *L. venusta*) indicated that the highest abundance was for *Cordia* (2.12 ± 0.23 spiders), followed by *Ceiba* (1.9 ± 0.2 spiders), and lastly *Swietenia* (1.18 ± 0.15 spiders). Mean abundances on *Cordia* and *Ceiba* did not differ significantly, but mean abundances on both of these species differed from those on *Swietenia* ($t_{1,14} > -4.71$, $P < 0.01$).

Overall, the above results indicated a clear differentiation in web-building spider assemblages among the tropical tree species studied. The observed patterns are noteworthy considering that at the time of sampling plants were two years old, and indicate that tree inter-specific variation in associated predator faunas may arise relatively early in tree ontogeny. In turn, the observed effects of tree species on spider communities are likely to further increase with tree age as new phenotypic features arise (e.g., increased architectural complexity).

This study's findings are consistent with findings from previous work in southern Mexico which reported that Theridiidae and Araneidae were the most species rich and abundant groups in both agricultural (Ibarra-Núñez & García-Ballinas 1998) and natural ecosystems (Maya-Morales et al. 2011). In addition, the most abundant species in our study, *Leucauge venusta*, has been reported, along with other species of the same genus (e.g., *L. mariana* (Taczanowski, 1881) and *L. argyra* (Walckenaer, 1841)), as a dominant web-building spider in cacao agroecosystems (De la Cruz et al. 2009) and coffee plantations (Pinkus-Rendón et al. 2006) in southern Mexico, as well as in managed ecosystems in temperate North America (Young & Edwards 1990). Species of the genus *Leucauge* White, 1841 build horizontal webs with a high number of radii and spirals which provide greater structural resistance (Dondale 2003) and also exhibit a broad diet breadth (De la Cruz et al. 2007), traits which have likely contributed to their colonization success and dominance.

The relative abundance and identity of common and rare web-building spiders exhibited marked differences among tree species. Biases in the preference for a particular tree species were especially evident for two of the most abundant spiders in our sample, *Araneus pegnia* and *Argiope argentata*. Field observations indicated that *Ara. pegnia* uses the leaves of *Cordia* for protection during the daytime by bending the leaf edges over them to create a shelter, whereas *Arg. argentata* uses the thorns of the main trunk on *Ceiba* as support structures to build their web and perhaps also as protection against other predators (L. Esquivel-Gómez, personal observation). These observations suggest that tree species variation in spider species recruitment was mediated (at least partly) by plant physical traits of leaves and stems (e.g., see Langelloto & Denno 2004; Jiménez-Valverde & Lobo 2007).

Variation in spider abundance between tree species could also have resulted from differences in the availability of web-building sites (i.e., attachment sites and branch or leaf arrangement; Jiménez-Valverde & Lobo 2007), shelters against other predators (Rypstra 1986), and microhabitat conditions (Rypstra 1986). For example, a higher abundance of orb weavers (Araneidae, Tetragnathidae) observed on *Cordia* and *Ceiba* could be explained because these species provide suitable habitat requirements such as a large separation between branches which allows the construction of the large-size webs (Stenchly et al. 2011). Plant size *per se* appeared not to be a main driver of differences in abundance, because *Cordia* was the smallest of the three species and exhibited the highest abundance. Further work is necessary to formally assess which physical traits are predictors of spider recruitment for the studied tree species. Interestingly, previous work conducted in the same experimental system reported no differences among tree species in the abundance of cursorial spiders

Table 1.—List of the web-building species sampled on the tropical trees Swietenia macrophylla ("sw"), Ceiba pentandra ("ce"), and Cordia dodecandra ("co"), in polyculture plots from a tree diversity experiment in southern Mexico (Yucatan). Total abundances are shown for each species of spider as well as spider abundances separately for each tree species. The top three most abundant spiders on each tree species are typed in bold.

Family	Species	Authority	key	sw	ce	co	total
Araneidae	*Acacesia hamata*	(Hentz, 1847)	Ah	0	0	2	2
	Araneus pegnia	(Walckenaer, 1842)	Ap	4	9	**41**	54
	Argiope argentata	(Fabricius, 1775)	Aa	3	**21**	1	25
	Cyclosa berlandi	Levi, 1999	Cb	3	**10**	3	16
	Cyclosa caroli	(Hentz, 1850)	Cc	1	8	2	11
	Eriophora ravilla	(C.L.Koch, 1844)	Er	**9**	3	6	18
	Gasteracantha cancriformis	(Linnaeus, 1758)	Gc	5	2	4	11
	Mangora itza	Levi, 2005	Mi	0	0	1	1
	Mecynogea lemniscata	(Walckenaer, 1842)	Ml	0	0	1	1
	Metepeira c. olmec	Piel, 2001	Mo	0	0	3	3
	Micrathena gracilis	(Walckenaer, 1805)	Mg	0	1	0	1
	Micrathena sagittata	(Walckenaer, 1842)	Ms	3	3	2	8
	Neoscona oaxacensis	(Keyserling, 1864)	No	0	1	1	2
	Verrucosa arenata	(Walckenaer, 1842)	Va	0	0	2	2
Theridiidae	*Achaearanea* sp.		Ach	1	0	0	1
	Achaearanea tesselata	(Keyserling, 1884)	Pt	1	1	0	2
	Ameridion signum	(Levi, 1959)	As	0	0	1	1
	Anelosimus studiosus	(Hentz, 1850)	Ans	0	1	0	1
	Argyrodes elevatus	Taczanowski, 1873	Ae	1	1	0	2
	Chrysso albomaculata	O.P. Cambridge, 1882	Ca	**8**	3	**12**	23
	Chrysso sp.		Cs	1	0	1	2
	Emertonella emertoni	(Bryant, 1933)	Ee	1	0	0	1
	Euryopis lineatipes	O.P. Cambridge, 1893	El	0	2	0	2
	Faiditus caudatus	(Taczanowski, 1874)	Fc	1	0	0	1
	Neospintharus rioensis	(Exline & Levi, 1962)	Ar	0	1	0	1
	Tidarren sisyphoides	(Walckenaer, 1842)	Ts	1	1	0	2
Tetragnathidae	*Leucauge venusta*	(Walckenaer, 1841)	Lv	**59**	**74**	**98**	231
Uloboridae	*Uloborus sp.*		Ulo	0	0	1	1
Total abundances				102	182	142	426

(Salticidae) (Abdala-Roberts et al. 2015), suggesting that tree species variation in web spider communities depends on traits associated with web construction.

Although direct effects of plant traits on spider recruitment are likely to be important for explaining our results, we cannot rule out the influence of indirect effects occurring through differences in herbivore abundance or diversity among tree species. Although spiders are generalist predators and frequently exhibit euryophagous behavior (Pekár et al. 2012), species vary largely in their hunting strategies and prey preferences (Nyffeler 1999). Some species build webs designed to capture specific prey such as adult Lepidoptera and ants and display oligophagous or even stenophagous behavior (Pekár et al. 2012). Thus, differences in herbivore composition among tree species would be expected to lead to variation in spider recruitment and species composition. Interestingly, *Swietenia* has the highest levels of leaf phenolics of the three tree species (S. Rosado-Sánchez unpublished) which may reduce insect herbivore abundance and diversity and in turn (at least partly) explain why spider abundance was lowest for this species. Further work is needed in order to determine the relative importance of direct vs. indirect effects of plant phenotypic variation on web-building spider communities.

Our findings have important implications provided that web-building spiders exert strong impacts on arthropod community structure. Reduced overlap among plant species in predator species composition is expected to lead to non-additive increments in predator diversity with increasing tree species diversity, as observed for spiders and other groups of predators in this experimental system (Campos-Navarrete et al. 2015; Esquivel-Gómez et al. in press). This may ultimately lead to higher predation rates. Indirect effects of spiders on plants may vary depending on the degree to which they feed upon other carnivorous vs. herbivorous arthropods, provided that spider top-down net effects on plants are positive. In that context, our results argue in favor of conserving tree diversity in forest patches and establishing mixed tree plantations to maintain or increase predator abundance and diversity, and to ultimately achieve top-down regulation of herbivore populations.

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